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Water use and growth responses of dryland wheat grown under elevated [CO_2] are associated with root length in deeper, but not upper soil layer

Shihab Uddin[a,b,*], Markus Löw[a], Shahnaj Parvin[b,c], Glenn Fitzgerald[a,d], Helale Bahrami[a], Sabine Tausz-Posch[a,e], Roger Armstrong[d,f], Garry O'Leary[d], Michael Tausz[c,g]

[a] Faculty of Veterinary and Agricultural Sciences, The University of Melbourne, 4 Water Street, Creswick, VIC, 3363, Australia
[b] Department of Agronomy, Bangladesh Agricultural University, Mymensingh, 2202, Bangladesh
[c] School of Ecosystem and Forest Sciences, The University of Melbourne, 4 Water Street, Creswick, VIC, 3363, Australia
[d] Department of Economic Development, Jobs Transport and Resources, Private Bag 260, Horsham, VIC, 3401, Australia
[e] School of Biosciences, University of Birmingham, Edgbaston, Birmingham, B15 2TT, UK
[f] Department of Animal, Plant and Soil Sciences, Centre for AgriBioscience, La Trobe University, Bundoora, VIC, 3086, Australia
[g] Birmingham Institute of Forest Research, University of Birmingham, Edgbaston, Birmingham, B15 2TT, UK

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ABSTRACT

This study investigated crop water use of wheat grown in a dryland Mediterranean-type environment under elevated atmospheric CO_2 concentrations ([CO_2]). Two related cultivars, contrasting in agronomic features (cvs. Scout and Yitpi; Scout has good early vigour and high transpiration efficiency), were grown under ambient [CO_2] (a[CO_2], ~400 µmol mol^{-1}) and elevated [CO_2] (e[CO_2], ~550 µmol mol^{-1}) in the Australian Grains Free Air CO_2 Enrichment (AGFACE) facility for two growing seasons. Each year, an irrigation treatment (rainfed versus irrigated) was imposed within the CO_2-treatments. Normalised difference vegetation index (as surrogate for canopy cover) and root length in the upper (0 cm–32 cm) and deeper (33 cm–64 cm) soil layers were measured at stem-elongation and anthesis.

Elevated [CO_2] stimulated root length of wheat in both upper and deeper soil layers, and this stimulation was modified by cultivars and irrigation regimes. Across cultivars and all treatments, water use, biomass and grain yield were positively associated with root length in the deeper soil layer but not with root length in the upper soil layer. The 'CO_2 fertilisation effect' on biomass and grain yield was of similar magnitude under both irrigated and rainfed conditions. Although e[CO_2] did not increase canopy cover in these experiments, the CO_2 effect on water use depended on cultivars and irrigation regimes. Despite greater e[CO_2]-induced stimulation of tillers and spikes, the cv. Scout did not receive more biomass or grain yield benefit from the 'CO_2 fertilisation effect' compared to cv. Yitpi.

1. Introduction

The concentration of atmospheric CO_2 ([CO_2]) has increased by just over 50% from the start of the Industrial Revolution (270 µmol mol^{-1}) (Long et al., 2004) to the current level (408 µmol mol^{-1}) in 2017 (NOAA, 2017). If CO_2 emissions continue at the current rate, atmospheric [CO_2] will reach 550 µmol mol^{-1} by the middle of this century (IPCC, 2013). As CO_2 is the main substrate of photosynthesis, this increase has direct implications for plant metabolism, such as stimulating net photosynthetic CO_2 assimilation in C_3 crops, leading to greater biomass production and yield through the so-called 'CO_2 fertilisation effect' (Ainsworth and Long, 2005; Ziska et al., 2012; Kimball, 2016).

This 'CO_2 fertilisation effect' on C_3 crops has been demonstrated in various agro-ecosystems (Ainsworth et al., 2002; Kimball et al., 2002; Long et al., 2006; Högy et al., 2009; Lam et al., 2012a,b; Hasegawa et al., 2013; Fitzgerald et al., 2016) but the extent of the fertilisation effect varies considerably across regions, as well as within the same region depending on environmental growing conditions (availability of nutrients and soil water, temperatures) (Leakey et al., 2012; McGrath and Lobell, 2013; Reich et al., 2014; Kimball, 2016). Free Air CO_2 Enrichment (FACE) systems have been established to investigate the plant-atmosphere relationship under future [CO_2]. However, such FACE systems focussing on plant or ecosystems responses to elevated [CO_2] (e[CO_2]) are scarce in arid and semi-arid areas because most are established in high rainfall temperate regions (Leakey et al., 2012; Rosenthal and Tomeo, 2013) or dealt with fully irrigated agro-ecosystems (Wall,

* Corresponding author at: Faculty of Veterinary and Agricultural Sciences, The University of Melbourne, 4 Water Street, Creswick, VIC, 3363, Australia.
E-mail address: shihab.uddin@unimelb.edu.au (S. Uddin).

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2001; Wall et al., 2001). There are strong theoretical reasons to assume arid or semi-arid agro-ecosystems will respond differently to e[CO_2] than the well-studied temperate regions, owing to, for example, low inputs of nutrients, low and very variable water supply, and reliance of crops on soil water reserves during hot and dry periods (Leakey et al., 2012). Modelling studies have identified substantial uncertainty around the magnitude and direction of crop response to e[CO_2] in water-limited Mediterranean-type environments (Ewert et al., 2002). Therefore, assessing the effect of e[CO_2] on crops in such environments is an important area of research.

Wheat (*Triticum aestivum* L.) is one of the most extensively grown grain crops in the world (Shewry, 2009). Approximately 15% of the global wheat producing area are located in low yielding, water limited Mediterranean-type environments (Fischer et al., 2014). In these environments wheat commonly has ample water supply during early growth stages, either from stored soil water or early season rainfall, but the grain filling period is often affected by extensive water shortage, termed terminal drought (Braun et al., 1996; Farooq et al., 2014), which is considered the major cause of grain yield variability of wheat in these regions (Tambussi et al., 2007; Dias de Oliveira et al., 2013). Under these conditions, additional water availability in the form of supplemental irrigation, conserved soil water from the early growth stages or sub-soil water acquisition through increased root length could potentially increase grain yields in wheat (Kirkegaard et al., 2007; Lilley and Kirkegaard, 2011).

Elevated [CO_2] might benefit water relations in wheat for two reasons in such Mediterranean-type environments: (1) through reducing stomatal conductance (g_s) and (2) through increasing root length. Reduced g_s under e[CO_2] increases instantaneous leaf level water use efficiency (Ainsworth and Long, 2005; Bernacchi et al., 2007), which may lower crop water use (Leakey et al., 2009; Kimball, 2016) during the early growth stages. This is hypothesised to increase available soil water during the grain filling period (Burkart et al., 2011; Hussain et al., 2013). Greater water availability under e[CO_2] reaching into the grain filling period may prolong physiological processes such as photosynthesis and thus result in greater growth (Wall et al., 2001). In contrast, excessive stimulation of early growth due to 'CO_2 fertilisation' may deplete soil water more quickly despite greater leaf level water use efficiency, and combined with reduced rainfall during grain filling as part of predicted future climates (CSIRO and Bureau of Meteorology, 2015; Watson et al., 2017), increase the risk of 'haying-off', where large early biomass production exhausts soil water and the crop dies off before grains are filled (van Herwaarden et al., 1998; Nuttall et al., 2012).

The second effect of e[CO_2] on water relations of crops particularly relevant to Mediterranean-type environments, is increased root length (Chaudhuri et al., 1990; VanVuuren et al., 1997; Benlloch-Gonzalez et al., 2014a,b; Bahrami et al., 2017), which may improve access to sub-soil water. Under water-limited conditions, access to sub-soil water provides an important buffer to unreliable in-season rainfall. Furthermore, the conversion efficiency of sub-soil water into grain yield is higher than that of in-season rainfall because it is taken up late in the crop growth cycle, during the critical grain-filling period when roots reach deeper layers (Kirkegaard et al., 2007; Wasson et al., 2012). Therefore, grain yield may respond strongly to even small amounts of additional sub-soil water that becomes accessible post-anthesis, because its uptake coincides with grain development when crops are vulnerable to terminal drought (Passioura, 1983).

Superior leaf level transpiration efficiency has been suggested as a promising trait for adapting wheat to semi-arid environments (Condon et al., 2004). It is defined as photosynthetic net CO_2 assimilation (A_{net}) divided by stomatal conductance (g_s) and higher transpiration efficiency is accomplished by either increased A_{net} and/or decreased g_s (Farquhar and Richards, 1984; Condon et al., 2004). A higher transpiration efficiency trait has been successfully implemented in commercial wheat cultivars (Condon et al., 2004). Transpiration efficiency is positively correlated with [CO_2], because rising [CO_2] increases A_{net} and decreases g_s, which ultimately improves transpiration efficiency (Ainsworth and Long, 2005; Ainsworth and Rogers, 2007; Bernacchi et al., 2007; Tausz-Posch et al., 2013). Even though e[CO_2] increases transpiration efficiency generally in wheat, a cultivar with a superior transpiration efficiency trait was shown to take greater advantage of the 'CO_2 fertilisation effect' than a near-isogenic cultivar with low transpiration efficiency (Tausz-Posch et al., 2012, 2013; Christy et al., 2018). Selection of traits, such as superior transpiration efficiency or deeper rooting for breeding CO_2-responsive crops may allow crops to take advantage of increased water use efficiency (WUE), biomass and yields of increasing atmospheric [CO_2].

Meta-analyses reported mean grain yield increases for wheat under e[CO_2] from 15 to 17% compared to a[CO_2] (Ainsworth and Long, 2005; Wang et al., 2013; Kimball, 2016). Most of these results were derived from FACE experiments in high yielding, high rainfall or continuously irrigated wheat growing systems where mean yields are commonly $> 5\,t\,ha^{-1}$ (Fitzgerald et al., 2016). The magnitude of relative yield stimulation by e[CO_2] is frequently predicted to be greater under drier than well-watered conditions (Leakey et al., 2009; McGrath and Lobell, 2013; Kimball, 2016), but a recent meta-analysis could not confirm this for drought stressed compared to well-watered crops (van der Kooi et al., 2016). Similarly, a recent long term evaluation of FACE results that included rain-out shelters to manipulate precipitation in the world's most productive agro-ecosystems showed that more intense drought diminished grain yield stimulation by e[CO_2] to zero (Gray et al., 2016). In a water limited agro-ecosystem, Houshmandfar et al. (2016) reported inter-seasonal variability of the 'CO_2 fertilisation effect' depending on the amount of rainfall, whereby grain yield stimulation of wheat by e[CO_2] was greater in a high rainfall than in a low rainfall year. However, because direct experimental evidence with side-by-side well-watered and drought treatments have not yet been conducted in dryland agro-ecosystems, it is not clear to what extent such previous results are direct consequence of water supply or related to possible other aspects of season-by-season variability.

To close this gap in current knowledge and also investigate the potential differences in water acquisition strategies between wheat cultivars under e[CO_2], we selected two commercial wheat cultivars with common genetic background but with contrasting agronomic features (vigour, grain size and transpiration efficiency). The experiments were conducted in the Australian Grains FACE (AGFACE) facility in the southeast Australian wheat belt, representative of Mediterranean or semi-arid, water limited, low yielding wheat cropping systems (Fitzgerald et al., 2016). This facility allowed us to study crops in the field and assess changes due to increased atmospheric [CO_2]. We tested the following hypotheses:

- Elevated [CO_2] will stimulate root growth and this greater root growth will be associated with better access to soil water in deeper layers.
- The 'CO_2 fertilisation effect' will be greater under irrigated than under rainfed conditions.
- Increased canopy cover caused by stimulation of biomass growth may nullify the benefit from greater leaf level water use efficiency under e[CO_2].
- A cultivar with a superior transpiration efficiency trait will capitalise more from the 'CO_2 fertilisation effect'.

2. Materials and methods

2.1. Plant materials

Wheat (*Triticum aestivum* L.) cultivars Scout and Yitpi were selected for their similar genetic background but contrasting agronomic (early vigour, grain size, transpiration efficiency) features (Houshmandfar et al., 2016; Bahrami et al., 2017). Yitpi is adapted broadly to most soil types and rainfall regions in southeast Australia, while Scout is a high

yielding mid-season line (Seednet, 2005). The cultivar Scout has the pedigree Sunstate/QH71-6/Yitpi and was developed by LongReach Plant Breeders. Scout was characterised as a cultivar with very good early vigour and improved transpiration efficiency (Pacificseeds, 2010; Hunt and Brill, 2012).

2.2. Experimental design

This experiment was conducted in 2014 and 2015 in the Australian Grains Free Air CO_2 Enrichment (AGFACE) facility in the Agriculture Victoria Plant Breeding Centre, Horsham (36°45′07″ S, 142°06′52″ E; 127 m elevation), Victoria, Australia. The study site has been described in detail by Mollah et al. (2009) and Fitzgerald et al. (2016). The experimental plots are on heavy Vertosol (Isbell, 1996) clay soil (~35% clay at the surface and 60% in 1.4 m depth). Detailed descriptions of soil physical and chemical properties are given in Lam et al. (2012a). The region has a Mediterranean-type climate with relatively dry, cool winters. Long-term (30-year: 1981–2010 period) average annual rainfall is 435 mm with 318 mm typically falling during the growing season of winter wheat (May – November). For the same time period, average maximum and minimum temperatures during the growing season were 17.8 °C and 5.3 °C respectively (Bureau of Meteorology, 2017). Maximum and minimum temperatures, as well as rainfall data during 2014 and 2015 growing seasons were recorded by an on-site weather station (MEA Premium Weather Station 103, Measurement Engineering Australia, Magill, SA, Australia) and are presented in Fig. 1.

The experimental design was a nested split-split-plot within a randomized complete block design (Supplementary Fig. S1) with four replicate plots ('rings') of 12 m diameter for a[CO_2] (~400 µmol mol^{-1}) and four rings for e[CO_2] (~550 µmol mol^{-1}). Within each ring, cultivars Scout and Yitpi were nested in two sub-plots of contrasting irrigation regimes, one under rainfed and another under irrigated (rainfed plus additional water supply to resemble well-watered) conditions. Each sub-plot was 4 m long, 1.4 m wide, and consisted of 6 rows with 0.244 m spacing. Plots were sown on 29 and 26 May in 2014 and 2015, respectively. At sowing, granular fertiliser (8.8% P, 11% S) was incorporated into the soil at rates of 7–9 kg P ha^{-1} and 8–11 kg S ha^{-1}. According to local practice, no N fertiliser was applied as the initial soil mineral nitrogen level in the profile (0–100 cm) was approximately 232 kg NO_3^--N ha^{-1}, which is considered high for the studied area (O'Leary et al., 2015; Bahrami et al., 2017; Tausz et al., 2017). Mean plant density as measured by seedlings counts at approximately 3–4 weeks after emergence was 94 ± 3.4 (mean ± SE of 64 plots) plants m^{-2}.

In the elevated rings, [CO_2] was enriched to reach a central target of 550 µmol mol^{-1} during daylight hours by injecting pure CO_2 into the air from the upwind side of a ring of horizontal stainless-steel tubes. The tubes were positioned about 150 mm above the canopy following the growth of the crop. The CO_2 mixed quickly with the ambient air as it was blown across the plot by the prevailing wind (Mollah et al., 2009). CO_2 concentrations were monitored and recorded every minute with an infrared gas analyser (IRGA, SBA-4, PP Systems, Amesbury, MA, USA) positioned at the centre of each ring. The median [CO_2] at the centre of e[CO_2] ring varied between 546 and 550 µmol mol^{-1} and concentrations were maintained at or above 90% of the target for 93–98% of the time during CO_2 injection (Mollah et al., 2009). The spatial variations of [CO_2] within the e[CO_2] rings were described by Mollah et al. (2011).

2.3. Irrigation regimes

Two irrigation regimes were applied: 'rainfed' and 'irrigated'. During the 2014 and 2015 growing seasons the site received very low rainfall (108 and 128 mm from sowing to harvest in 2014 and 2015, respectively, compared to the long-term average seasonal rainfall of 318 mm). To keep the crop alive until maturity, the 'rainfed' treatment received some additional irrigation (94 mm in 2014 and 96 mm in 2015) during the growing season. In contrast, the irrigated sub-plots received additional 304 mm and 268 mm irrigation in 2014 and 2015, respectively, in approximately weekly intervals (Fig. 1). To achieve uniform and high germination rates, 34 mm of irrigation was applied before sowing to both rainfed and irrigated sub-plots, in both years.

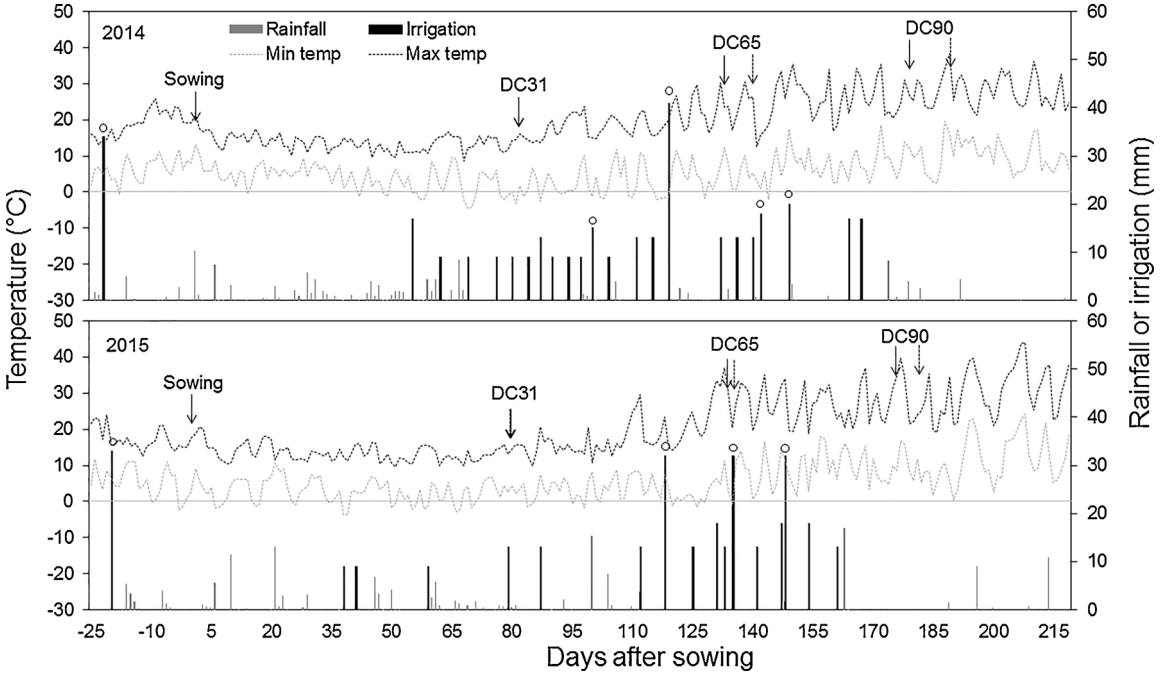

Fig. 1. Rainfall, irrigation and temperatures recorded on-site in 2014 and 2015 growing seasons in the Australian Grains Free Air CO_2 Enrichment (AGFACE) facility, Horsham, Victoria, Australia. Arrows indicate sowing, stem-elongation (growth stage DC31 according to Zadoks et al., 1974), anthesis (DC65), and maturity (DC90) of rainfed (continuous line) and irrigated (broken line) wheat. Irrigation bars with circle on top represent irrigation events applied to both in the rainfed and irrigated sub-plots.

2.4. Water use (WU)

Seasonal water use (WU) was calculated using a water balance equation as follows (Li et al., 2013):

$$WU\ (mm) = P + I - D + CR - R + SWD \quad (1)$$

Where, P is precipitation (mm), I is irrigation (mm), D is deep drainage from the root zone (mm), CR is capillary rise to the root zone (mm), R is runoff, and SWD is soil water depletion (mm) in the 100 cm profile. SWD was the difference between the gravimetric soil water content at sowing and at harvest. Sampling took place in increments of 10 cm up to 40 cm depth and thereafter in 20 cm increments using a hydraulically operated soil sampler. Deep drainage and runoff were insignificant for this location, and were considered zero (Angus and van Herwaarden, 2001; O'Leary et al., 2015). Due to a deep ground water table, capillary rise was also considered zero. Consequently, Eq. (1) was simplified as follows:

$$WU\ (mm) = P + I + SWD \quad (2)$$

2.5. Normalised difference vegetation index (NDVI)

Non-destructive measurements of canopy reflectance, from which the Normalised difference vegetation index (NDVI) was calculated, were acquired with a CropCircle ACS-210 with GeoSCOUT GLS-400 data logger (Holland Scientific, Lincoln, NE, USA). Measurements were taken at stem-elongation (DC31; (Zadoks et al., 1974)) and anthesis (DC65). The sensor was held 1.5 m above the soil surface and oriented to measure a foot-print across the middle four rows of the plot. The NDVI is calculated directly by the sensor and mean values of transects from non-disturbed areas within the sub-plot were used as a surrogate for canopy cover (Fitzgerald, 2010; Perry et al., 2012).

2.6. Root length

Root length was measured with a mini-rhizotron root growth monitoring system (CI-600™, CID Bio-Science Inc., Camas, WA, USA) (Taylor et al., 1990) at DC31 and DC65. Detailed description of installing acrylic clear mini-rhizotron tubes and acquiring the images of root system for the same experimental set-up is given in Bahrami et al. (2017). In short: one 1.05 m long mini-rhizotron tube was preinstalled at 45° in each of four sub-plots per ring. For each rhizotron access tube four images were captured from depths, ~0–16, 17–32, 33–48, and 49–64 cm below the soil surface. The images were analysed for the captured root length per image using the software RootSnap!™ version 1.2.8.23 (CID Bio-Science Inc., Camas, WA, USA). Root length values of the top two (0–32 cm) and the bottom two (33–64 cm) depths are reported as upper and deeper soil layer root length, respectively. We make no claim to quantify root biomass or length accurately on a plot basis, but report root length per mini-rhizotron tube to compare relative effects of treatments. Bulk density, pH, organic carbon, soil water status and other physiochemical properties of upper and deeper soil layers of the study site are reported in the supplementary Table S1.

2.7. Growth, yield and morphological parameters

To determine plant biomass and morphological parameters, destructive sampling took place at DC31 (in 2015 only), DC65 and at physiological maturity (DC90). At DC65 and DC90 a predetermined sub-plot of 0.73 m^2 was harvested that included the middle 4 of 6 rows in a sub-plot. At DC31, 10 plants per plot were randomly sampled and the biomass was adjusted m^{-2} based on plant density of the respective sub-plot. At DC65, leaves (cut off at the ligule) were separated from the stems (including leaf sheaths) and then oven-dried for 72 h at 70 °C. At DC90, samples were dried for 72 h at 40 °C and were separated into spikes and straw (stems and leaves together). The spikes were threshed to separate grains and chaff. Tiller and spike number and thousand grain weight (TGW) were also recorded. All biomass and yield data are given as dry weight (zero % moisture). Harvest Index (HI) was calculated as grain yield divided by total dry biomass at DC90. Water use efficiency of biomass (WUEb) and grain yield (WUEy) were calculated by dividing biomass and grain yield by water use.

2.8. Statistical analysis

The experimental design was a nested split-split-plot within a randomized complete block design with 2 [CO_2] (main-plots) × 2 irrigation regimes (sub-plot, irrigation regimes within ring) × 2 cultivars (sub-sub-plot, cultivars within irrigation regimes) × 4 replicates (rings), hence, 2 × 2 × 2 × 4 = 32 experimental plots in each of the two years. The effect of CO_2, irrigation regimes, and cultivars were considered fixed effects and year and ring as random effects in linear mixed effects models evaluated with the R package 'nlme' (Pinheiro et al., 2018). Homogeneity of variances was evaluated visually and the model was adjusted when stepwise evaluation of the model showed an improvement. Simple regression analyses with R software were used to assess the relationship between water use and other parameters under a [CO_2] and e[CO_2]. Statistical effects were regarded significant at $P < 0.1$. Data analysis was performed in R version 3.4.3 (R Core Team, 2017).

3. Results

3.1. Root length

At DC31, e[CO_2] increased root length in the upper soil layer by 24% but had no effect on root length in the deeper soil layer ($P = 0.732$, Fig. 2). Supplemental irrigation decreased the root length in the upper soil layer by 27%, but increased it in the deeper soil layer more than three-fold (338%).

At DC65, root length in the upper soil layer was 34% greater under e[CO_2] than a[CO_2] (Fig. 3). Under both a[CO_2] and e[CO_2] root length of cv. Yitpi in the same layer was 53% greater than cv. Scout. Irrigation regimes had no significant effect ($P = 0.131$) on root length in the upper soil layer. In the deeper soil layer, root length was significantly affected by CO_2, irrigation and cultivar interactions (CO_2 x IR x Cv: $P = 0.028$; Fig. 3). Elevated [CO_2] increased the root length of cv. Scout in the deeper soil layer under irrigated conditions by 49% but decreased it by 46% under rainfed conditions. Root length of cv. Yitpi in the deeper soil layer showed the opposite response of cv. Scout, whereby e[CO_2] increased the root length by 170% under rainfed conditions and decreased it by 12% under irrigated conditions. Averaging across all treatments, root length in the deeper soil layer at DC65 was significantly (all $P < 0.001$) correlated with biomass at DC65 ($R^2 = 0.681$) and DC90 ($R^2 = 0.632$), grain yield ($R^2 = 0.641$) and water use ($R^2 = 0.661$, Fig. 4). There was no correlation between root length in the upper soil layer and these parameters.

3.2. Normalised difference vegetation index and biomass

At DC65, NDVI was 43% higher under irrigated compared to rainfed conditions (Fig. 5). Leaf dry weight was greater (94%) for wheat grown under irrigated than rainfed conditions (Fig. 5). Cultivar Yitpi had 17% greater leaf weight than cv. Scout. CO_2-treatments had no significant effect on NDVI ($P = 0.171$) and leaf dry weight ($P = 0.883$) at DC65. Aboveground biomass at DC65 was 19% greater for wheat grown under e[CO_2] than a[CO_2].

Supplemental irrigation increased the biomass at DC65 by 54%. Leaf weight at DC65 ($R^2 = 0.703$), biomass at DC65 ($R^2 = 0.585$), biomass at DC90 ($R^2 = 0.738$), grain yield ($R^2 = 0.787$) and water use ($R^2 = 0.816$) were significantly (all $P < 0.001$) correlated with NDVI

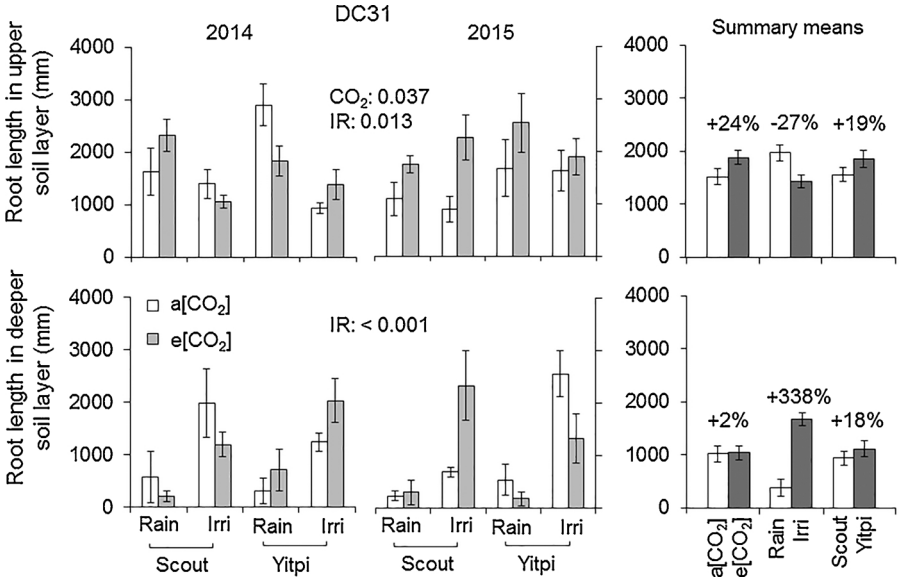

Fig. 2. Captured root length (per mini-rhizotron tube) in the upper (0–32 cm) and deeper (33–64 cm) soil layers of wheat (*Triticum aestivum* L.) cvs. Scout and Yitpi at stem-elongation (DC31) grown under ambient [CO_2] (a[CO_2], ~400 µmol mol^{-1}) or elevated [CO_2] (e[CO_2], ~550 µmol mol^{-1}) in rainfed (Rain) or irrigated (Irri) conditions in 2014 and 2015 in the Australian Grains Free Air CO_2 Enrichment (AGFACE) facility, Horsham, Victoria, Australia. Data are mean values and standard errors of n = 4. P < 0.10 are reported for fixed effects CO_2, irrigation regime (IR) and cultivar (Cv) and their interactions from a mixed effects model with year used as random effect (not listed effects: P ≥ 0.10). In the right panels, summary means and the percentage changes (left to right column) are reported for main fixed effects (means and standard errors of n = 32; significance see left panel).

at DC65 (Fig. 6). Seasonal water use showed significant (P < 0.001, R^2 = 0.585) and positive correlation with leaf weight at DC65 (Fig. 6). At DC31, neither CO_2 nor irrigation regimes had significant effect on NDVI and biomass. At this stage, biomass of early vigour cv. Scout was 10% greater than cv. Yitpi (P = 0.097; data not shown).

3.3. Water use and water use efficiency

Under rainfed conditions, water use of cv. Scout was 13% higher under e[CO_2] compared to a[CO_2], but under irrigated conditions, cv. Scout used 7% less water under e[CO_2] compared to a[CO_2] (Table 1). Under both irrigation regimes, water use of a[CO_2] and e[CO_2] grown Yitpi did not differ (CO_2 x IR x Cv, P = 0.022). Both WUEb and WUEy of wheat grown under e[CO_2] was 13% greater than under a[CO_2], regardless of irrigation regimes or cultivars (Table 1).

3.4. Yield and yield components

Wheat grown under irrigated conditions produced 25% and 29% more tillers and spikes, respectively, than in rainfed conditions (Tables 1 and 2). Elevated [CO_2] increased both tiller (12%) and spike (9%) numbers of cv. Scout but these decreased (by 5–7%) for cv. Yitpi (CO_2 x Cv, P = 0.027 for tillers and P = 0.041 for spikes). Thousand grain weight (TGW) of cv. Yitpi was greater than that of cv. Scout. Elevated [CO_2] increased the TGW under both irrigation regimes but to a greater (8%) extent under irrigated than (3%) rainfed conditions (CO_2 x IR, P = 0.061). At maturity, e[CO_2] increased both biomass and grain yield to a similar extent (~14%). Stimulation by e[CO_2] of biomass and grain yield did not differ between irrigation regimes and cultivars (no significant CO_2 x IR or CO_2 x Cv interactions observed for these two parameters). Irrigation resulted in more biomass (72%) and grain yield (80%) compared to rainfed conditions. There was no significant difference in biomass and grain yield between the two cultivars (Table 2). The HI of cv. Scout was 4% greater than that of cv. Yitpi (Table 1). Plants grown under irrigated conditions had greater (8%) HI compared to rainfed conditions. Biomass (R^2 = 0.789) and grain yield (R^2 = 0.820) at DC90 were significantly (all P < 0.001) and positively correlated with seasonal water use (Fig. 7).

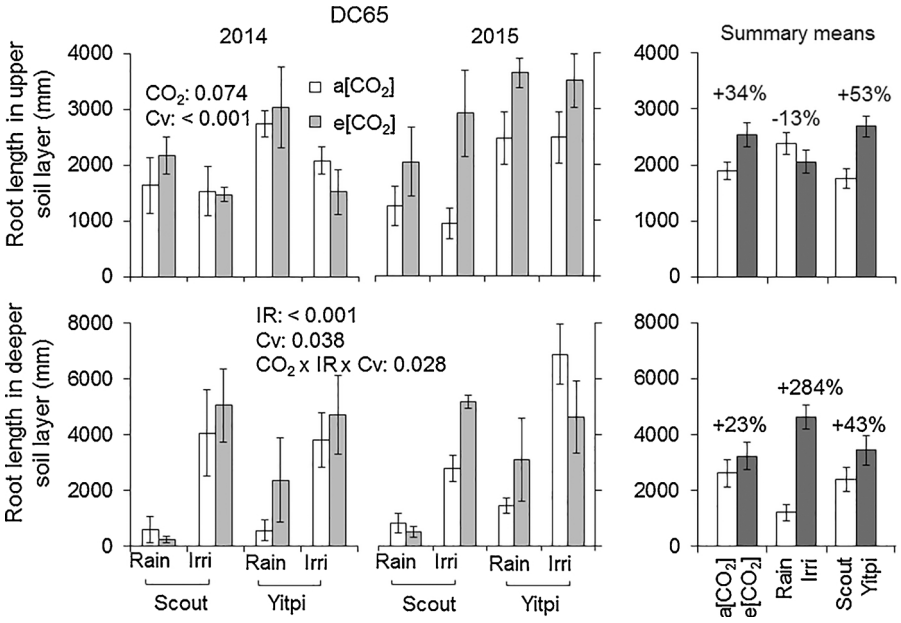

Fig. 3. Captured root length (per mini-rhizotron tube) in the upper (0–32 cm) and deeper (33–64 cm) soil layers of wheat (*Triticum aestivum* L.) cvs. Scout and Yitpi at anthesis (DC65) grown under ambient [CO_2] (a[CO_2], ~400 µmol mol^{-1}) or elevated [CO_2] (e[CO_2], ~550 µmol mol^{-1}) in rainfed (Rain) or irrigated (Irri) conditions in 2014 and 2015 in the Australian Grains Free Air CO_2 Enrichment (AGFACE) facility, Horsham, Victoria, Australia. Data are mean values and standard errors of n = 4. P < 0.10 are reported for fixed effects CO_2, irrigation regime (IR) and cultivar (Cv) and their interactions from a mixed effects model with year used as random effect (not listed effects: P ≥ 0.10). In the right panels, summary means and the percentage changes (left to right column) are reported for main fixed effects (means and standard errors of n = 32; significance see left panel).

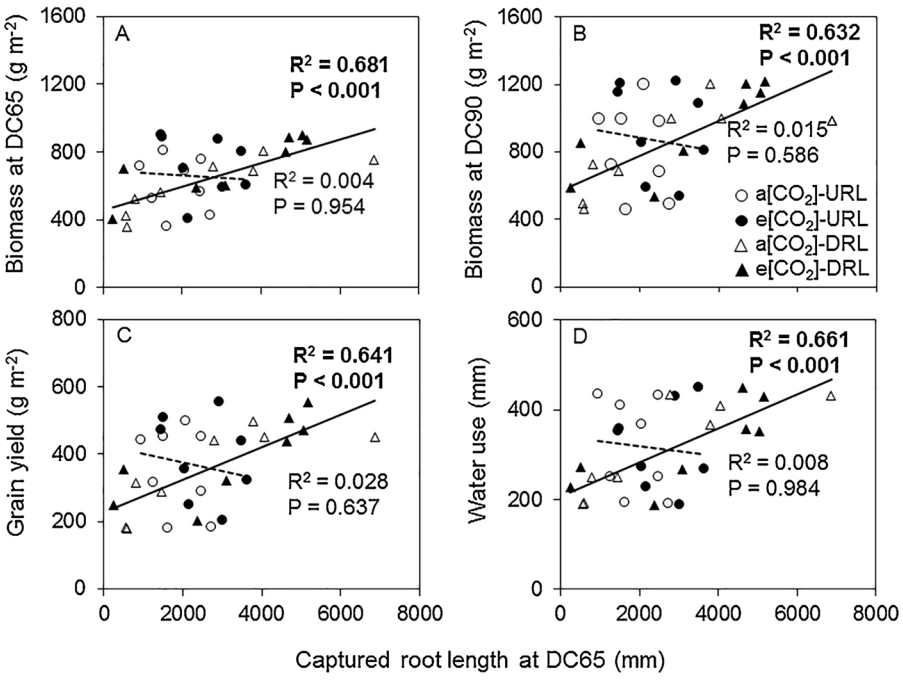

Fig. 4. Linear regressions between captured root lengths in the upper (URL; broken line and R^2 and P in normal font) or deeper (DRL; continuous line and R^2 and P in bold font) soil layers at DC65 and biomass at DC65 (A), biomass at DC90 (B), grain yield (C) and water use (D) of wheat (*Triticum aestivum* L.) cvs. Scout and Yitpi grown under ambient [CO_2] (a[CO_2], ~400 µmol mol^{-1}) or elevated [CO_2] (e[CO_2], ~550 µmol mol^{-1}) with rainfed or irrigated conditions in 2014 and 2015 in the Australian Grains Free Air CO_2 Enrichment (AGFACE) facility, Horsham, Victoria, Australia. Each data point is mean values of n = 4.

4. Discussion

4.1. Phenological development

Winter rainfall in the major cropping regions of Victoria was significantly lower than the long-term seasonal average for both studied years and many local farmers had to either abandon or cut most of their crops for hay. In both studied years 'rainfed' plots received supplemental irrigation to prevent complete crop failure. Despite such supplemental irrigation, grain yield under rainfed condition was significantly lower than under irrigated conditions. Under such water limited conditions phenological development is one of the most important features for crop adaptation and yield (Richards, 2006; Sadras and Monzon, 2006; Passioura, 2007; Sacks and Kucharik, 2011). Drought, temperature and [CO_2] are important environmental factors affecting the rate of plant growth, development and crop growth duration (Sadras and Monzon, 2006; Bahuguna and Jagadish, 2015; Ihsan et al., 2016; Jagadish et al., 2016). Consistent with earlier FACE studies under water limited conditions (Kimball et al., 1995; Fitzgerald et al., 2016) no visible effect of [CO_2] on phenological development was detected. However, accelerated development from onset of flowering and through the grain filling period were observed under rainfed

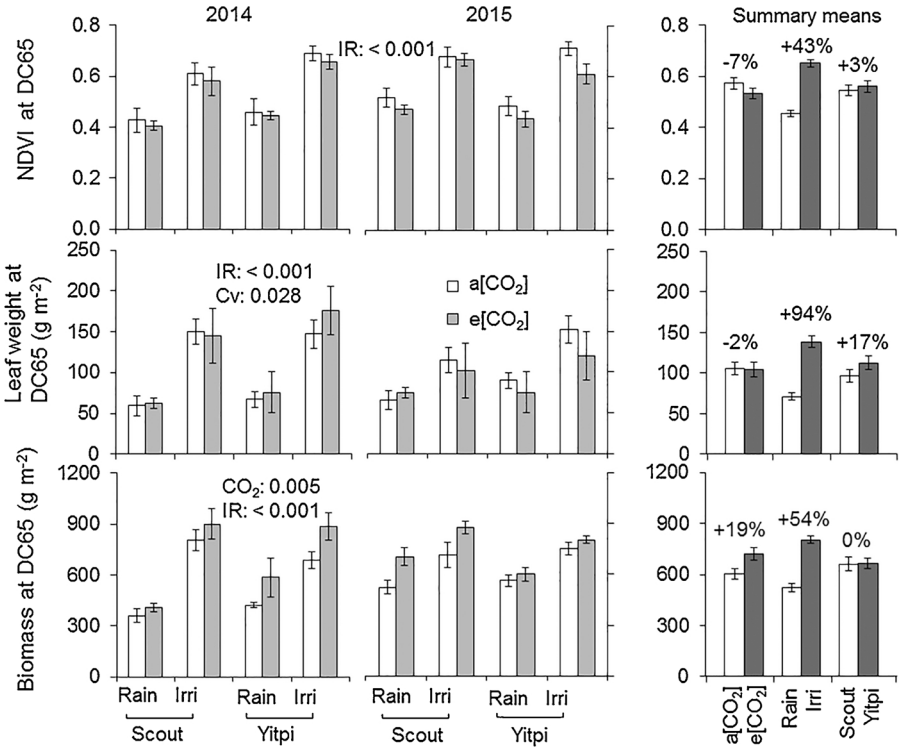

Fig. 5. NDVI, leaf weight and biomass of wheat (*Triticum aestivum* L.) cvs. Scout and Yitpi at anthesis (DC65) grown under ambient [CO_2] (a[CO_2], ~400 µmol mol^{-1}) or elevated [CO_2] (e[CO_2], ~550 µmol mol^{-1}) in rainfed (Rain) or irrigated (Irri) conditions in 2014 and 2015 in the Australian Grains Free Air CO_2 Enrichment (AGFACE) facility, Horsham, Victoria, Australia. Data are mean values and standard errors of n = 4. P < 0.10 are reported for fixed effects CO_2, irrigation regime (IR) and cultivar (Cv) and their interactions from a mixed effects model with year used as random effect (not listed effects: P ≥ 0.10). In the right panels, summary means and the percentage changes (left to right column) are reported for main fixed effects (means and standard errors of n = 32; significance see left panel).

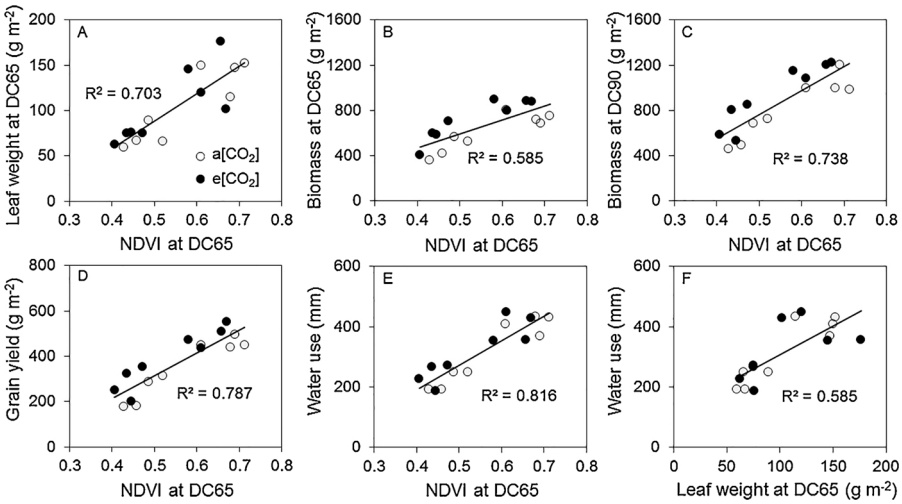

Fig. 6. Linear regressions ($P < 0.001$ for all parameters) between NDVI at DC65 and leaf weight at DC65 (A), biomass at DC65 (B), biomass at DC90 (C), agrain yield (D) and water use (E) as well as between leaf weight at DC65 and water use (F) of wheat (*Triticum aestivum* L.) cvs. Scout and Yitpi grown under ambient [CO_2] (a[CO_2], ~400 µmol mol^{-1}) or elevated [CO_2] (e[CO_2], ~550 µmol mol^{-1}) with rainfed or irrigated conditions in 2014 and 2015 in the Australian Grains Free Air CO_2 Enrichment (AGFACE) facility, Horsham, Victoria, Australia. Each data point is mean values of n = 4.

relative to irrigated conditions (Fig. 1), which is in line with earlier studies (Ihsan et al., 2016). Dry conditions shorten the grain filling period and thereby lower the grain yield (Sadras and Monzon, 2006; Ihsan et al., 2016) as also observed in the present study.

4.2. Greater root growth under e[CO_2] was associated with greater water use, presumably because of better access to water in deeper soil layers

The e[CO_2]-stimulation of root length observed in our study is in line with trends generally observed in CO_2 enrichment studies (Chaudhuri et al., 1990; Wechsung et al., 1999; Madhu and Hatfield, 2013; Benlloch-Gonzalez et al., 2014a,b; Bahrami et al., 2017). Elevated [CO_2] stimulated root growth in the upper soil layer during vegetative growth (DC31) showing that e[CO_2] began to establish differences in growth early in the season. In the upper soil layer about 77% of the root length was established by this stage but most of the deeper soil roots were established between DC31 and DC65 (root length at DC31 was only 35% of DC65). Elevated [CO_2] stimulated the total root growth at DC65 by stimulating root length both in upper and deeper soil layers, indicating the stimulation of root weight and/or length under e[CO_2] is present throughout the life cycle of wheat, whereby differences are often most pronounced at DC65 (Wechsung et al., 1999; Bahrami et al., 2017). For wheat, root length, as well as uptake functions are usually maximal at DC65 and decrease thereafter until maturity (Wechsung et al., 1995; Asseng et al., 1998; Lampurlanés et al., 2001; Wang et al., 2014; Bahrami et al., 2017), as later in the season most of the assimilates are used for reproductive growth (Gregory and Atwell, 1991). Therefore, biomass and grain yield at DC90 were correlated with the root length at DC65.

Increased root growth in a well-watered deeper layer can: 1) make significant contributions to maintaining physiological processes even when the upper layer is subjected to drought (Gallardo et al., 1994; Uddin et al., 2017) and 2) allow more water extraction during grain filling (Manschadi et al., 2006). Deeper roots are younger and more efficient in extracting and taking up water compared to roots in upper layers (Gregory et al., 1978) and during the grain filling period a larger portion of roots die in the upper soil layers compared to deeper layers (Pritchard et al., 2006). Averaged across both years, irrigation regimes and cultivars, e[CO_2] stimulated the root length in both upper and deeper soil layers. Consistent with earlier studies (Chaudhuri et al., 1990; VanVuuren et al., 1997; Madhu and Hatfield, 2013) this stimulation was somewhat greater in the upper than the deeper soil layers.

In our study, both water use and root length in the deeper soil layer were affected by a complex interaction between CO_2, cultivar and irrigation. Despite such complex interactions, water use was positively correlated with root length in the deeper soil layer across all experimental variants. In contrast, the absence of such a relationship between water use and root length in the upper soil layer further indicated the importance of deeper roots, as they enable access to soil water at depth, which resulted in greater water use, biomass and grain yield. Water captured by roots in deeper soil layers is particularly valuable since its provision coincides with the grain filling period and has a high conversion efficiency into grain yield (Passioura, 1983; Angus and van Herwaarden, 2001; Kirkegaard et al., 2007). The vertical distribution pattern of roots and its effect on access to deeper soil water is a key trait for improved adaptation of wheat in dryland Mediterranean regions (Manschadi et al., 2006), particularly given the increase in root growth under e[CO_2].

The response of root growth to e[CO_2] can depend on cultivar (Benlloch-Gonzalez et al., 2014a) and/or growing conditions (Chaudhuri et al., 1990; Wechsung et al., 1999; Pritchard et al., 2006). In contrast with some earlier studies where cultivars with early vigour were reported to have deeper and bigger root systems (Richards and Lukacs, 2002; Liao et al., 2004), we observed greater root length in cv. Yitpi at DC65 than in cv. Scout, which purportedly exhibits early vigour. Even at DC31, the early vigour cv. Scout did not have greater root length than cv. Yitpi. Similarly, Bahrami et al. (2017) studying seasonal root growth pattern of the same wheat cultivars, did not observe greater e[CO_2]-induced stimulation of root length for cv. Scout than cv. Yitpi, in any growth stages. Although the early vigour trait in cv. Scout was not expressed in our growing conditions, a study with experimental wheat lines expressing strong early vigour traits reported even suppression of root growth by e[CO_2] in the vigorous lines (Benlloch-Gonzalez et al., 2014a).

4.3. The 'CO_2 fertilisation effect' was similar under irrigated and rainfed conditions

It has been a long-held paradigm that because of the positive effect of e[CO_2] on water use efficiency, crops will profit more from e[CO_2] under drought conditions (Leakey et al., 2009; McGrath and Lobell, 2013; Kimball, 2016). Recent results challenge this view even in the most productive agro-ecosystems and indicate that intensive drought may preclude any benefit from the 'CO_2 fertilisation effect' (Gray et al., 2016; Jin et al., 2018), and some recent studies have reported greater biomass and grain yield stimulation by e[CO_2] in wetter rather than drier growing conditions (Houshmandfar et al., 2016). In our study, we therefore hypothesised that e[CO_2]-induced stimulation of biomass and grain yield would be greater with additional water supplied by irrigation. This hypothesis was not confirmed, as the 'CO_2 fertilisation effect' on biomass and grain yield was similar under both irrigated and rainfed conditions without a significant CO_2 x IR interaction for biomass or

Table 1
Biomass, yield, yield components and water use efficiencies at physiological maturity (DC90) of wheat (*Triticum aestivum* L.) cvs. Scout and Yitpi grown under ambient [CO_2] (a[CO_2], ~400 μmol mol^{-1}) or elevated [CO_2] (e[CO_2], ~550 μmol mol^{-1}) in rainfed (Rain) or irrigated (Irri) conditions in 2014 and 2015 in the Australian Grains Free Air CO_2 Enrichment (AGFACE) facility, Horsham, Victoria, Australia. Data are mean values and standard errors of n = 4. Summary means and the percentage change (%Δ) are reported for the main fixed effects CO_2, irrigation regime (IR) and cultivar (Cv). Positive %Δ indicates increases of response variables from a[CO_2] to e[CO_2], cv. Scout to cv. Yitpi and rainfed to irrigated. TGW: thousand grain weight.

Response parameters				Tillers (# m^{-2})	Spikes (# m^{-2})	TGW (g)	Grain yield (g m^{-2})	Biomass (g m^{-2})	Harvest Index (%)	Water use (mm)	WUEb (g biomass m^{-2} mm^{-1})	WUEy (g grain yield m^{-2} mm^{-1})
2014	Scout	Rain	a[CO_2]	273.9 ± 33.7	254.1 ± 34.3	39.7 ± 1.4	178.2 ± 32.1	458.4 ± 77.2	0.39 ± 0.01	191.7 ± 6.3	2.4 ± 0.3	0.9 ± 0.1
			e[CO_2]	324.1 ± 18.3	285.5 ± 15.8	39.2 ± 2.3	249.5 ± 14.1	585.9 ± 55.4	0.40 ± 0.01	227.5 ± 20.6	2.7 ± 0.4	0.9 ± 0.3
		Irri	a[CO_2]	381.5 ± 17.9	378.4 ± 14.0	43.1 ± 2.0	449.8 ± 40.6	1000.8 ± 108.8	0.45 ± 0.01	409.0 ± 5.0	2.5 ± 0.3	1.1 ± 0.1
			e[CO_2]	444.3 ± 33.7	410.2 ± 30.3	43.7 ± 2.1	471.5 ± 64.2	1149.1 ± 177.4	0.41 ± 0.01	353.0 ± 25.9	3.2 ± 0.3	1.3 ± 0.1
	Yitpi	Rain	a[CO_2]	321.0 ± 52.1	293.0 ± 51.2	39.5 ± 2.4	181.8 ± 36.9	496.3 ± 97.0	0.37 ± 0.01	191.3 ± 9.6	2.6 ± 0.6	0.9 ± 0.2
			e[CO_2]	271.5 ± 22.1	240.8 ± 22.1	41.4 ± 2.6	200.6 ± 7.8	533.1 ± 29.6	0.37 ± 0.01	187.1 ± 15.5	2.9 ± 0.4	0.9 ± 0.3
		Irri	a[CO_2]	408.5 ± 40.6	417.4 ± 41.0	41.8 ± 2.1	496.0 ± 31.3	1203.2 ± 63.8	0.41 ± 0.02	368.0 ± 15.7	3.3 ± 0.2	1.4 ± 0.1
			e[CO_2]	392.1 ± 48.3	364.1 ± 37.2	47.3 ± 2.1	508.3 ± 57.5	1205.4 ± 138.2	0.42 ± 0.01	356.4 ± 31.3	3.4 ± 0.5	1.5 ± 0.2
2015	Scout	Rain	a[CO_2]	335.4 ± 50.4	307.4 ± 37.2	39.4 ± 0.8	315.4 ± 40.0	724.9 ± 75.8	0.43 ± 0.02	250.6 ± 13.2	2.9 ± 0.3	1.3 ± 0.2
			e[CO_2]	363.7 ± 29.8	335.7 ± 19.0	41.1 ± 0.8	354.5 ± 16.4	855.3 ± 38.1	0.41 ± 0.01	272.3 ± 20.7	3.2 ± 0.1	1.3 ± 0.1
		Irri	a[CO_2]	366.8 ± 17.8	350.4 ± 6.5	40.0 ± 0.5	440.3 ± 30.3	996.3 ± 83.5	0.44 ± 0.01	434.7 ± 14.5	2.3 ± 0.2	1.0 ± 0.1
			e[CO_2]	393.8 ± 10.2	378.4 ± 8.6	44.1 ± 0.4	552.6 ± 24.9	1220.3 ± 68.3	0.45 ± 0.01	427.9 ± 15.1	2.9 ± 0.2	1.3 ± 0.1
	Yitpi	Rain	a[CO_2]	335.7 ± 65.0	299.9 ± 34.9	42.8 ± 1.3	288.6 ± 41.6	687.8 ± 76.7	0.41 ± 0.02	250.8 ± 7.5	2.8 ± 0.4	1.2 ± 0.2
			e[CO_2]	359.0 ± 10.0	334.7 ± 13.7	43.8 ± 0.8	322.5 ± 25.5	808.6 ± 42.3	0.40 ± 0.01	266.9 ± 10.9	3.0 ± 0.1	1.2 ± 0.1
		Irri	a[CO_2]	432.0 ± 33.5	378.4 ± 13.7	41.9 ± 0.8	450.3 ± 28.7	987.1 ± 67.0	0.46 ± 0.02	430.7 ± 15.4	2.3 ± 0.1	1.0 ± 0.1
			e[CO_2]	403.0 ± 26.1	356.6 ± 34.1	44.6 ± 0.8	437.9 ± 36.3	1085.1 ± 86.4	0.40 ± 0.00	449.0 ± 12.3	2.4 ± 0.2	1.0 ± 0.1
Summary means		CO_2	a[CO_2]	356.9 ± 13.0	334.9 ± 13.3	41.0 ± 0.6	350.0 ± 24.0	819.4 ± 51.7	0.42 ± 0.01	315.8 ± 18.1	2.6 ± 0.1	1.1 ± 0.05
			e[CO_2]	368.9 ± 12.3	338.2 ± 11.8	43.1 ± 0.0	398.0 ± 23.5	930.0 ± 54.6	0.41 ± 0.0	317.5 ± 17.0	3.0 ± 0.1	1.3 ± 0.04
			%Δ	+3	+1	+5	+14	+14	−2	+1	+13	+13
		IR	Rain	323.0 ± 11.1	293.9 ± 10.7	40.9 ± 0.6	263.8 ± 15.1	643.8 ± 32.0	0.40 ± 0.01	229.8 ± 7.4	2.8 ± 0.1	1.1 ± 0.05
			Irri	402.7 ± 9.9	379.2 ± 9.2	43.3 ± 0.6	475.8 ± 14.6	1105.9 ± 37.1	0.43 ± 0.0	403.6 ± 8.7	2.8 ± 0.1	1.2 ± 0.05
			%Δ	+25	+29	+6	+80	+72	+8	+76	−1	+4
		Cv	Scout	360.4 ± 11.4	337.5 ± 11.0	41.3 ± 0.6	380.6 ± 23.8	873.9 ± 53.8	0.43 ± 0.01	320.8 ± 17.1	2.7 ± 0.1	1.2 ± 0.04
			Yitpi	365.4 ± 13.9	335.6 ± 14.0	42.9 ± 0.7	365.9 ± 24.4	875.8 ± 54.3	0.41 ± 0.01	312.5 ± 18.0	2.8 ± 0.1	1.2 ± 0.05
			%Δ	+1	−1	+4	−4	0	−4	−3	+4	−1

Table 2
P-values for the fixed effects CO_2, irrigation regime (IR) and cultivar (Cv) as well as their interactions are reported from a mixed effects model with year used as random effect for the reported parameters in Table 1 and Figs. 2, 3 and 5 at three growth stages, stem-elongation (DC31), anthesis (DC65) and maturity (DC90) of wheat. Statistically significant ($P < 0.1$) effects are shown in bold numbers. RL: root length, TGW: thousand grain weight.

Effect	DC31		DC65					DC90						
	RL in upper soil layer	RL in deeper soil layer	RL in upper soil layer	RL in deeper soil layer	NDVI	Leaf weight	Biomass	Tillers	Spikes	TGW	Grain yield	Biomass at DC90	Harvest index	Water use	WUEb	WUEy
CO_2	**0.037**	0.732	**0.074**	0.329	0.171	0.883	**0.005**	0.542	0.859	0.115	**0.062**	**0.073**	0.200	0.897	**0.081**	**0.069**
IR	**0.013**	**< 0.001**	0.131	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**	**0.035**	**< 0.001**	0.884	0.503
Cv	0.129	0.180	**< 0.001**	**0.038**	0.261	**0.028**	0.973	0.711	0.880	**0.007**	0.438	0.965	**0.036**	0.176	0.498	0.815
$CO_2 \times$ IR	0.804	0.729	0.805	0.844	0.781	0.629	0.764	0.941	0.569	**0.061**	0.622	0.874	0.528	**0.013**	0.717	0.867
$CO_2 \times$ Cv	0.234	0.491	0.429	0.873	0.431	0.958	0.893	**0.027**	**0.041**	0.266	0.214	0.301	0.517	0.621	0.404	0.307
IR × Cv	0.216	0.737	0.221	0.541	0.279	0.495	0.162	0.576	0.896	0.486	0.583	0.553	0.962	0.600	0.774	0.554
$CO_2 \times$ IR × Cv	0.424	0.226	0.344	**0.028**	0.406	0.572	0.949	0.774	0.569	0.685	0.602	0.632	0.169	**0.022**	0.350	0.422

grain yield, or water use efficiencies. Consistent with our results, a modelling study on earlier AGFACE results also failed to find consistent CO_2 and irrigation interactions on biomass and grain yield of wheat (O'Leary et al., 2015). Furthermore, a recent meta-analysis that summarised only experiments where drought and well-watered treatments were compared side by side found similar effect sizes for the 'CO_2 fertilisation' (van der Kooi et al., 2016). Comparing 'dry' with 'wet' growing seasons to assess CO_2 x water interactions, as done by some of the above cited reports may be fundamentally different from the side-by-side irrigation treatment in a dry background environment as in our study, because other variables will also be different when comparing 'wet' with 'dry' seasons. It is important to better define 'dry' and 'wet' growing seasons, because timing of water supply may also be important for the CO_2 effect (Gray et al., 2016; Houshmandfar et al., 2016). Although irrigation in our study maintained soil water to a largely 'unstressed' extent, crops may have still experienced a form of temporary drought stress through periods of high vapour pressure deficit, which will not occur during natural rainfall events. The type of drought stress (in terms of soil drying and rewetting patterns) has been shown to potentially determine CO_2 responses of crops (Gray et al., 2016), and especially in dryland environments, vapour pressure deficit and soil water dynamics may affect outcomes in more complex ways.

4.4. Canopy cover under e[CO_2] was unchanged and so did not alter the benefit from greater leaf level water use efficiency

Water use is strongly correlated with canopy cover and increased canopy cover can lead to greater water use under e[CO_2] (Samarakoon and Gifford, 1995; Gray et al., 2016), which agrees with results in our study across [CO_2], cultivars and irrigation regimes. Although CO_2 and cultivar had no significant effect at any of the growth stages studied on canopy cover (NDVI) or leaf weight, the effect of e[CO_2] on water use depended on cultivars and irrigation regimes (Tables 1 and 2). In our study, e[CO_2] reduced water use only under irrigated conditions, which is in line with some earlier studies (Leakey et al., 2009; Burkart et al., 2011; Hussain et al., 2013; Kimball, 2016) and may be due to reduction in stomatal conductance (Bernacchi et al., 2007; Burkart et al., 2011; Houshmandfar et al., 2016). The lack of water savings by e[CO_2] under rainfed conditions might be due to the severe drought experienced in both years. In both years, rainfed crops only received one third of the long-term average water supply, and this might have resulted in all available soil water being used up. Depletion of soil water under rainfed conditions causes stomata to close much of the time and therefore e[CO_2] may have very little or no effect on stomatal conductance (Wall et al., 2001, 2011) and thus seasonal water use (Kimball, 2016). Under intense drought conditions, water savings by e[CO_2] are diminished to zero and water use is increased even in the most productive agro-ecosystems in temperate region (Gray et al., 2016). However, small or no change in water use when coupled with the increased biomass and grain yield under e[CO_2] results in greater WUE (Hunsaker et al., 2000). In the current study, observed WUE for both biomass and yield were greater under e[CO_2] than a[CO_2], and as grain yields were correlated with water use this indicates that higher concentrations of CO_2 created a system with more efficient use of water under both rainfed and irrigated conditions.

4.5. No clear differences between cultivars regarding benefits from the 'CO_2 fertilisation effect'

Knowledge of intra-specific variability in yield response to e[CO_2] is a key prerequisite for breeding to maximise CO_2 response (Tausz et al., 2013; Bishop et al., 2015). Genotypic variability in response to e[CO_2] has been reported for soybean (Bishop et al., 2015), peanut (Ziska et al., 2016), rice (Uprety et al., 2003; Hasegawa et al., 2013) and wheat (Tausz-Posch et al., 2012; Ziska et al., 2012), where increased grain yield under e[CO_2] was associated with greater number of tillers, spikes

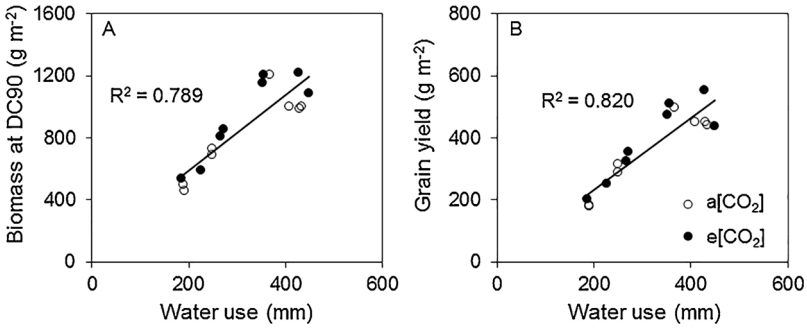

Fig. 7. Linear regressions ($P < 0.001$ for all parameters) between water use and biomass at DC90 (A) and grain yield (B) of wheat (*Triticum aestivum* L.) cvs. Scout and Yitpi grown under ambient [CO_2] (a[CO_2], ~400 µmol mol^{-1}) or elevated [CO_2] (e[CO_2], ~550 µmol mol^{-1}) with rainfed or irrigated conditions in 2014 and 2015 in the Australian Grains Free Air CO_2 Enrichment (AGFACE) facility, Horsham, Victoria, Australia. Each data point is mean values of n = 4.

and kernels spike^{-1} and/or greater grain size, all traits that ensure an appropriate 'sink capacity' (growing organs using assimilates) to capitalise from the 'CO_2 fertilisation' (Tausz-Posch et al., 2015).

Earlier studies in AGFACE using two near-isogenic cultivars with contrasting transpiration efficiency reported greater e[CO_2]-induced grain yield stimulation for the high transpiration efficiency cultivar, especially in low yielding conditions (Tausz-Posch et al., 2012; Christy et al., 2018). The cultivars compared in this present study had a common genetic background, but differed in several agronomic traits including early vigour, grain size as well as transpiration efficiency as marked by a carbon isotope technique (Condon et al., 2004). Therefore, we hypothesised, early vigour and transpiration efficient cv. Scout will capitalise more from the 'CO_2 fertilisation effect' than cv. Yitpi. This hypothesis was not confirmed, as the 'CO_2 fertilisation effect' did not differ between studied cultivars. At DC31, greater (10%; $P = 0.097$) biomass of cv. Scout than cv. Yitpi might be attributed from its early vigour trait, which disappeared in subsequent harvests. At final harvest, e[CO_2] increased both tiller and spike number of cv. Scout to a greater extent compared to cv. Yitpi, but this did not result in greater biomass or grain yield gain under e[CO_2] for cv. Scout than cv. Yitpi, confirming earlier results for the same two cultivars across two very contrasting growing seasons (Houshmandfar et al., 2016). As the lack of interactions between CO_2 and cultivar for grain yield shows, the greater e[CO_2]-stimulation of tiller and spike number of cv. Scout over cv. Yitpi were offset by fewer kernels spike^{-1} and/or smaller grain size, emphasising the importance of trade-offs and trait combinations. Increasing [CO_2] will, on average and as long as other changes do not nullify the 'CO_2 fertilisation effect', increase grain yields, but the right combination of traits could allow crops to capitalise on this effect to the greatest extent possible.

5. Conclusions

We can confirm our first hypothesis, as e[CO_2] stimulated root length of wheat in both upper and deeper soil layers, but only roots located deeper in the profile were positively associated with biomass, grain yield and water use, whereas those located in the upper profile were not. Along with a lack of CO_2-stimulation of cover and leaf biomass, but increased WUE, total biomass and yield across irrigated and rainfed conditions under e[CO_2], we conclude that rooting at deeper depths under e[CO_2] allows crops under dryland conditions to take greater advantage of limited sub-soil water than under current [CO_2]. We could however not confirm our second hypothesis, because yield and biomass response to e[CO_2] in this experiment was similar between the two irrigation regimes. With regard to our third hypothesis, our results showed a significant positive correlation between canopy cover and water use, but because there was no consistent e[CO_2]-effect on canopy cover and green leaf dry weight, the effect of e[CO_2] on water use was inconsistent between cultivars and irrigation regimes. And finally, we could not confirm our fourth hypothesis, because there were no consistent differences between cultivars in their responses to the 'CO_2 fertilisation effect'. Failure to clearly confirm or reject hypotheses 2 and 4 may be due to large environmental effects that mask small differences between cultivars or small differences in responses to irrigation regimes in this dryland environment.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.fcr.2018.05.014.

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